Determination of biological reference points for Bristol Bay red king crab

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Abstract

The US Magnuson–Stevens Fishery Conservation and Management Act mandates precautionary management to attain near maximum sustainable yield (MSY)-producing stock and exploitation levels on a long-term basis. Various biological reference points (BRPs) have been suggested as surrogates for MSY-producing instantaneous fishing mortality (F_{MSY}) and total stock biomass (SSB(F_{MSY})), which are largely derived from finfish biological and fisheries characteristics, for poorly understood stocks. BRP estimation for some crab fisheries has been complicated by the fact that only males are harvested and that recruitment, in many instances, is largely driven by environmental factors rather than density-dependent responses. For managing Bering Sea and Aleutian Islands crab stocks, instantaneous natural mortality (M) is used as a proxy for F_{MSY}, and mean annual total mature stock biomass during 1983–1997 is used for SSB(F_{MSY}). In this paper, harvest rate- and biomass-based BRPs were determined using crab-specific parameters for Bristol Bay red king crab (*Paralithodes camtschaticus*). Effective spawning stock biomass-per-recruit for combined sexes was estimated by length-based analysis and used in conjunction with Beverton–Holt and Ricker stock–recruit (S–R) models for various parametric values to explore the trends in MSY-producing legal male harvest rate at the time of the fishery ($E(F_{MSY})$), as a proportion of stock harvested; $\log_{10}$ of (F_{MSY}/M) ratio; and total mature stock biomass ratio SSB(F_{MSY})/SSB(0), where SSB(0) was the virgin total mature stock biomass. The F_{MSY} exceeded M for most cases. For a plausible S–R shape parameter (τ) range = 0.3–0.5, M = 0.3, handling mortality proportion = 0.2, and instantaneous bycatch mortality = 0.01; the SSB(F_{MSY}) ranged from 58 to 74% of SSB(0) for the mating ratio 1:1, and 40–55% of SSB(0) for the mating ratio 1:3. The $E(F_{MSY})$ ranged 16–35% for the mating ratio 1:1, and 40–79% for the mating ratio 1:3. The $E(F_{MSY})$ was more sensitive to mating ratio and handling mortality than bycatch mortality. Considering the uncertainty in stock parameters and recruitment, a precautionary legal male target harvest rate below 18% was suggested to rebuild the stock equal to or above 66% of the pristine total mature biomass.
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1. Introduction

A biological reference point (BRP) is a conventional value of fishing mortality (F) or stock biomass (B) defined on the basis of biological parameters and the characteristics of which are thought to be useful for managing the stock. It can be derived by quantitative analysis or assigned an arbitrary value and is often specified without variance (Jakobsen, 1992; Caddy and Mahon, 1995; Quinn and Deriso, 1999). For a number of fish and invertebrate stocks, either the pertinent data are lacking or analyses are unfeasible for determining optimal harvest strategies that will lead to long-term maximum sustainable yield (MSY). Biological reference points that require limited data or analysis or that can be borrowed from

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Nomenclature

a and b	parameters in the weight–length model
$\bar{B}(F)_t$ and $\bar{B}(0)_t$	average effective spawning biomasses (adjusted for male to female mating ratio) in a cohort corresponding to a fishing mortality F (for legal males) and $F = 0$ (for females or sublegal males) in year t, respectively
BYM	constant annual instantaneous bycatch mortality
$c(F)_t$	sum of catches in all size groups of legal males in a cohort in number corresponding to a fishing mortality F in year t
$C(F)$	sum of $c(F)_t$ through the fishery life span (i.e., stock catch in number), from t_r to λ
CL_{up} and CL_{low}	upper and lower size limits, respectively, of a length-class l for mean weight at size calculation
e	base of natural logarithms
$E(F_{MSY})$	exploitation rate of legal males at the time of the fishery corresponding to a fishing mortality F_{MSY}
$ESB(F)$, $ESB(F_{MSY})$ and $ESB(0)$	effective total (males plus females) spawning stock biomasses (adjusted for male to female mating ratio) corresponding to a fishing mortality F, F_{MSY} and $F = 0$, respectively
$(ESB/R)_F$ and $(ESB/R)_{F=0}$	effective total spawning stock biomass-per-recruit corresponding to a fishing mortality F and $F = 0$, respectively
$(ESB/R)_{ESB=0}$	effective total spawning stock biomass-per-recruit determined as the reciprocal of the slope at the origin of the stock–recruitment (S–R) curve
F	constant instantaneous fishing mortality for a biological year t
F_{MSY}	constant instantaneous fishing mortality that will produce MSY at the MSY-producing biomass
$FSSB(0)$	sum of average effective spawning biomass of mature female crab over an average fishery life span (i.e., effective spawning stock biomass of females) corresponding to a zero (direct) fishing mortality on females
$FSSN(0)$	sum of average mature female crab abundances in number over an average fishery life span (i.e., mature female stock abundance) corresponding to a zero fishing mortality
g and d	parameters in the logistic moulting probability model
GHL	guideline harvest level
h	proportion of sublegal males and females died due to capture and release to sea (i.e., mortality due to handling of sublegal male and all female crabs)
HM	constant annual instantaneous handling mortality (defined as a function of F with h and sublegal catchability as parameters in Appendix B)
j'	size interval index for recruit and post-recruit male crabs for catch estimation
$\bar{l}$	mean of x
l_2 and l_1	lower and upper limits, respectively, of a receiving length interval l for $P_{l',l}$ estimation
m_l	molting probability in a length-class l (estimation method using a logistic model is described in Appendix B)
M	constant annual instantaneous natural mortality
$MSSB(F)$	sum of average effective spawning biomass of mature legal and sublegal male crab over an average fishery life span (i.e., effective spawning stock biomass of males) corresponding to a fishing mortality F on legal males

MSSN(F)	sum of average mature legal and sublegal male crab abundances in number over an average fishery life span (i.e., mature male stock abundance) corresponding to a fishing mortality F on legal males
MSST	minimum total spawning stock biomass, equivalent to a half of MSY-producing biomass
n	total number of length intervals available in a cohort for $P_{l',l}$ estimation
$N(F)_{l,t}$ and $N(0)_{l,t}$	abundances in numbers in a length-class l of a cohort corresponding to a fishing mortality F (for legal males) and $F = 0$ (for females or sublegal males) in year t, respectively
$\bar{N}(F)_t$ and $\bar{N}(0)_t$	average abundances in numbers in a cohort corresponding to a fishing mortality F (for legal males) and $F = 0$ (for females or sublegal males) in year t, respectively
$P_{l',l}$	probability of crabs in a length group l' growing into a length group l (estimation method using a normal probability model is described in Appendix B)
$R(F)$, $R(F_{MSY})$ and $R(0)$	numbers of recruits to male pre-recruit 1 and female class 1 size groups produced by ESB(F), ESB(F_{MSY}) and ESB(0), respectively
R_{max}	asymptotic (maximum) recruitment, set to 2000 for per-recruit analysis
s	standard deviation of x
SSB(F), SSB(F_{MSY}), and SSB(0)	nominal (unadjusted for male to female mating ratio) total mature stock biomass corresponding to a fishing mortality F, F_{MSY}, and $F = 0$ on legal males, respectively
t_r	relative age at recruitment in year
T	average time elapsed between the mid survey date (stock enumeration date; i.e., start of a biological year) and start date of a fishing period as a fraction of a year
$W(F_{MSY})$ and $W(0)$	mean weights of individuals in the MSY-producing biomass and virgin biomass, respectively
W_l	mean weight of crabs in a length-class l
x	a normal random variable representing the annual growth increment
X	ESB(F_{MSY})/ESB(0) ratio
$y(F)_t$	sum of catches in all size groups of legal males in a cohort in weight corresponding to a fishing mortality F in year t
$Y(F)$	sum of $y(F)_t$ through the fishery life span (i.e., stock catch in weight), from t_r to λ
Z_{MSY}	$F_{MSY} + M$, constant instantaneous total mortality
Greek letters	
α, β, γ, and θ	parameters in the S–R models
δ	duration of average fishing period as a fraction of a year (handling and fishing mortality occur during this time period, hence *HM* and annual fishing mortality values are scaled to this period)
λ	relative maximum age of a cohort in year
τ	a parameter (Tau) estimated from a spawning biomass-per-recruit ratio, which influences the steepness near the origin and overall shape of the S–R curve, referred to as the S–R shape parameter in this paper (but Mace (1994) named it as the extinction parameter)
$\tau_{l'}$	mid length of a providing length interval l' for $P_{l',l}$ estimation

a similar population have been utilised to formulate sustainable harvest policies for these stocks. For example, because of inadequate data or limited analysis, fisheries management plans developed under the US Magnuson–Stevens Fisheries Conservation and Management Act for a number of commercially important crab stocks in the Bering Sea and Aleutian Islands (BSAI) consider natural mortality (M) to be equal to MSY-producing fishing mortality (F_{MSY}). The spawning stock biomass-producing MSY (SSB(F_{MSY})) is determined as the 1983–1997 average of the annual total stock biomass of mature male and female crabs estimated by annual resource assessment surveys (NPFMC, 1999).

The BRPs for BSAI crab stocks are directly borrowed from groundfish management plans without considering differences in growth, reproductive behaviour and fisheries characteristics between crab and groundfish stocks, which may result in different BRP levels (of threshold biomass and exploitation rate) between the two groups. Although crab-specific life history characteristics may warrant different types of BRPs, specific biological information required to quantify those BRPs at a broader stock level for monitoring purpose is either currently not available or data are very limited for most crab stocks. For example, sperm limitation may have a greater effect on recruit production than does mature biomass in some Canadian east coast snow crab (*Chionoecetes opilio*) stocks, but there is a difficulty in quantifying this characteristic at a stock level for monitoring purposes (Bernard Sainte-Marie, Crustacean Section, Fisheries and Oceans Canada, Quebec, Canada G5H 3Z4; personal communication). The two groundfish-based BRPs, a threshold exploitation rate and a threshold biomass, have been used in the BSAI crab management for sometime because the first is determinable from biological and fisheries information while the second is estimable from annual resources survey (Stevens et al., 2000a,b). However, they have not been estimated by rigorous analyses. Thus, the primary purpose of this paper is to develop methods to estimate the two BRPs using crab-specific growth, mortality and reproductive characteristics. In particular, an effective total spawning stock biomass is defined, which is either a whole or part of female plus male mature stock biomass estimated by adjusting for male to female mating ratio, and it is assumed to be solely responsible for recruit production (Justification for this definition is given in Section 2.2.). Thus, a crab-specific mating characteristic is incorporated in the method. The other purpose of this paper is to highlight the shortcoming of M as a default proxy for F_{MSY}.

Maintaining F at the M value is believed to produce yields near MSY (Alverson and Pereyra, 1969; Gulland, 1970). Hence, M has been used as a default proxy for F_{MSY}. The shortcomings of this approach have been addressed by a number of scientists (Francis, 1974; Deriso, 1982; Thompson, 1992). Francis (1974), considering the logistic production model, showed that $F_{MSY} = M$ only under very limited conditions. The F_{MSY} could be higher or lower than M depending on whether the maximum number of recruits was lower or higher than that at F_{MSY}. Deriso (1982), using a delay-difference population model, concluded that MSY exploitation fraction was less than M for a range of population growth values. Thompson (1992), considering a family of dynamic pool models and certain stock–recruitment (S–R) and weight-at-age relationships, argued that F_{MSY} could be higher or lower than M depending on the shape of the S–R curve. In this paper, the relationship between F_{MSY} and M as discussed by Francis (1974) and Thompson (1992) was further explored under general biomass growth and mortality conditions, and F_{MSY} was derived as a function of M for application to any finfish or shellfish stock that follows the Beverton and Holt (1957) dynamic pool model.

To demonstrate the BRP estimation methods using crab-specific biological and fisheries characteristics, published biological and fisheries parameters of Bristol Bay red king crab (*Paralithodes camtschaticus*), a reasonably well-studied stock in the Bering Sea, were used in computer simulations to explore trends in various BRPs—MSY-producing fishing mortality, harvest rate and mature stock biomass.

2. Methods and materials

2.1. F_{MSY} to M relationship

The exact formulation of the F_{MSY} to M relationship (modified from Francis (1974) and Thompson (1992), Appendix A) under general biomass growth

and cohort decline models is given below. This is a general formula applicable to any finfish or shellfish stock that satisfies the assumptions listed in Appendix A:

$$F_{\text{MSY}} = \left[\frac{W(F_{\text{MSY}})R(F_{\text{MSY}})(1 - e^{-Z_{\text{MSY}}(\lambda - t_{\text{r}})})}{XW(0)R(0)(1 - e^{-M(\lambda - t_{\text{r}})})} - 1 \right] M \tag{1}$$

The F_{MSY} can be estimated in terms of M by solving the nonlinear equation (1) for given values of $R(F_{\text{MSY}})/R(0)$, $W(F_{\text{MSY}})/W(0)$, and X ratios; λ, and t_{r}. For data-poor and less-investigated stocks, plausible values of those parameters are hard to obtain. On the other hand, with limited biological information, the length-based per-recruit model can be used to explore the trends in BRPs for various mortality and recruitment parametric values and to restrict the results to plausible ranges. The length-based simulation procedure is described in the next section.

2.2. F_{MSY}, $E(F_{\text{MSY}})$, and $SSB(F_{\text{MSY}})/SSB(0)$ determination

Mace (1994) derived a set of formulas based on spawning stock biomass-per-recruit to investigate the trends in various BRPs, including F_{MSY} and $SSB(F_{\text{MSY}})$, for finfish types of stock parameters under Beverton and Holt (1957) and Ricker (1954) S–R models. This procedure was extended to the Bristol Bay red king crab stock to explore the trends in $E(F_{\text{MSY}})$, which is a function of F_{MSY}, $\log_{10}(F_{\text{MSY}}/M)$ and $SSB(F_{\text{MSY}})/SSB(0)$ ratio for different mortality values, male:female mating ratio, and S–R relationships.

The $E(F_{\text{MSY}})$ formula modified from Gulland (1983) is as follows:

$$E(F_{\text{MSY}}) = \left(\frac{F_{\text{MSY}}}{F_{\text{MSY}} + (M + BYM)\delta} \right)$$
$$\times (1 - e^{-(F_{\text{MSY}} + (M + BYM)\delta)}) \tag{2}$$

The length-based method was used to simulate $(ESB/R)_F$ for recruit and then yield predictions with the published Bristol Bay red king crab biological and fisheries parameters as follows.

The simulation was initiated with 1000 males at pre-recruit 1 size (one growth increment below recruit size, but mature) and 1000 females at class 1 size (one growth increment below the class 2 size, but mature) to estimate $(ESB/R)_F$ to generate recruit numbers (i.e., number of pre-recruit 1 males and class 1 females) through an S–R model and then to estimate legal male yield from those recruits. The fishery selectively target on male component of the stock, but there are known fishery impacts related to handling mortality on the sublegal males and females. The females, which were not retained in the catch, were labelled as class 1 and class 2 size categories. The Bristol Bay red king crab size categories used in the simulations are described in Section 2.3.

In this paper, an effective total (combined sexes) spawning stock biomass was computed to generate recruits. This is a modification from that of Zheng et al. (1995a,b) who considered the female component of the stock adjusted for male spawning potential as the $ESB(F)$ for red king crab S–R modelling. The $ESB(F)$ definition as effective total spawning stock biomass has some merits for one or more of the following reasons: (1) Paul and Paul (1997), from a laboratory study, found that most male red king crabs ≥ 140 mm CL could fertilise three mates during the brief period when most multiparous females breed. Sperm limitation appears to limit recruit production in some crab species (e.g., some snow crab stocks in the east coast of Canada (see Bernard Sainte-Marie's personal communication in Section 1). Thus, since the amount of sperm passed by mating males has a direct relationship with the amount of fertilised eggs, it is prudent to consider the mating ratio and include the male spawning biomass in the effective spawning biomass calculation. (2) A number of red king crab researchers have considered the option of including males in their S–R models (e.g., Matulich et al., 1990; Greenberg et al., 1991). Greenberg et al. obtained the best S–R fit when males were included. (3) Bristol Bay red king crab mature female abundance estimates have larger errors compared to those of males (e.g., see Stevens et al., 2000b; Rugolo et al., 2001); consequently, relying only on the female component may introduce large errors in the $ESB(F)$ estimates and hence management decisions. (4) Although different spawning biomass definitions (females, males, females plus males) are likely to change the parameters of a given S–R model, the overall goodness of fit of the model may not differ much. For example,

Zheng et al. (1995a) considered alternative spawning indices (total females and total males plus females) and found R^2 to be close among the S–R fits. (5) Fishing mortality affects both components of the stock, directly in the case of legal males and indirectly in the case of sublegal males and all females. Variation in the sex ratio at different fishing mortality levels may also affect recruitment, in particular when there are limitations on the number of mating males and the amount of sperm to fertilise sufficient number of eggs for successful recruitment. The per-recruit analysis presented in this paper accounted for the effect of varied sex ratio in determining ESB(F) by $(ESB/R)_F$.

The male crabs in each of pre-recruit 1 size intervals may remain in the same size interval, or grow to the higher size intervals as a result of annual moult followed by growth. Male crabs in any size interval will remain in the same size interval next year, if they skip moult or moult with insufficient growth to move into a larger size interval. All female crabs were assumed to moult annually (Zheng et al., 1995a); so, female crabs in any size interval will remain in the same size interval next year, if they moult with insufficient growth to move into a larger size interval. The abundances in each size interval are also affected by annual mortality.

The length-based models used to capture these growth and mortality characteristics are described in Appendix B. It provides steps to calculate ESB(F) and $(ESB/R)_F$, which were the basis of harvest rate- and total mature biomass-based BRP estimation. Both BRPs are determinable with limited biological and fisheries data and resources survey information. Fig. 1 provides a flow chart showing analysis steps to derive various BRPs.

Recruitment was modelled using the following two well-known stock–recruitment models (Eq. (3), Beverton and Holt (1957); Eq. (4), Ricker (1954)):

$$R(F) = \frac{ESB(F)}{\alpha + \beta\, ESB(F)} \tag{3}$$

$$R(F) = \gamma\, ESB(F)\, e^{-\theta\, ESB(F)} \tag{4}$$

The $R_{\max}$ for Beverton and Holt S–R relationship is $1/\beta$, and that for Ricker S–R relationship is $\gamma\, e^{-1}/\theta$. The $R_{\max}$ was set at 2000.

Mace (1994) provided the extinction (or S–R shape) parameter, τ, as

$$\tau = \frac{(ESB/R)_{ESB=0}}{(ESB/R)_{F=0}} \tag{5}$$

$(ESB/R)_{ESB=0}$ equals to α for the Beverton and Holt S–R model and $1/\gamma$ for the Ricker stock–recruitment model. Therefore, for the Beverton and Holt S–R model:

$$\alpha = \tau\left(\frac{ESB}{R}\right)_{F=0}, \tag{6}$$

and

$$\gamma = \frac{1}{\tau(ESB/R)_{F=0}} \tag{7}$$

for the Ricker S–R model. Thus, for a given τ and a fixed $R_{\max}$, all parameters of the S–R relationships can be determined from an estimate of $(ESB/R)_{F=0}$. The slope of the Beverton and Holt S–R curve near the origin is $1/\alpha$ and that of Ricker is γ; therefore, near the origin, τ is inversely proportional to the slope for both types of S–R curves. Hence, by varying the τ value, different steepness (near the origin) and shape of the S–R curve can be obtained. The biological significance of τ is that, at low spawning biomass levels, the drop in recruitment with decrease in biomass (i.e., the rate of decline of recruitment) is much steeper when the τ value is smaller for a stock.

For BRP estimation, the $R(F)$, ESB(F), and various proportions for the two S–R models were estimated from $(ESB/R)_F$ for a fixed growth matrix and varying levels of mortality parameters. Table 1 provides those estimation formulas.

To estimate the catch, $R(F)$ estimated from either Eqs. (8) or (9) in Table 1 was equally divided into pre-recruit 1 males and class 1 females, and legal male catch ($c(F)_t$ and $y(F)_t$) during a biological year t was generated from only male recruits of the cohort using the following equations:

$$c(F)_t = \left(\frac{F}{F + (M + BYM)\delta}\right)\left(\sum_{j'=4}^{10} N(F)_{j',t}\right)$$
$$\times e^{-MT}(1 - e^{-(F+(M+BYM)\delta)}) \tag{16}$$

$$y(F)_t = \left(\frac{F}{F + (M + BYM)\delta}\right)\left(\sum_{j'=4}^{10} N(F)_{j',t} W_{l'}\right)$$
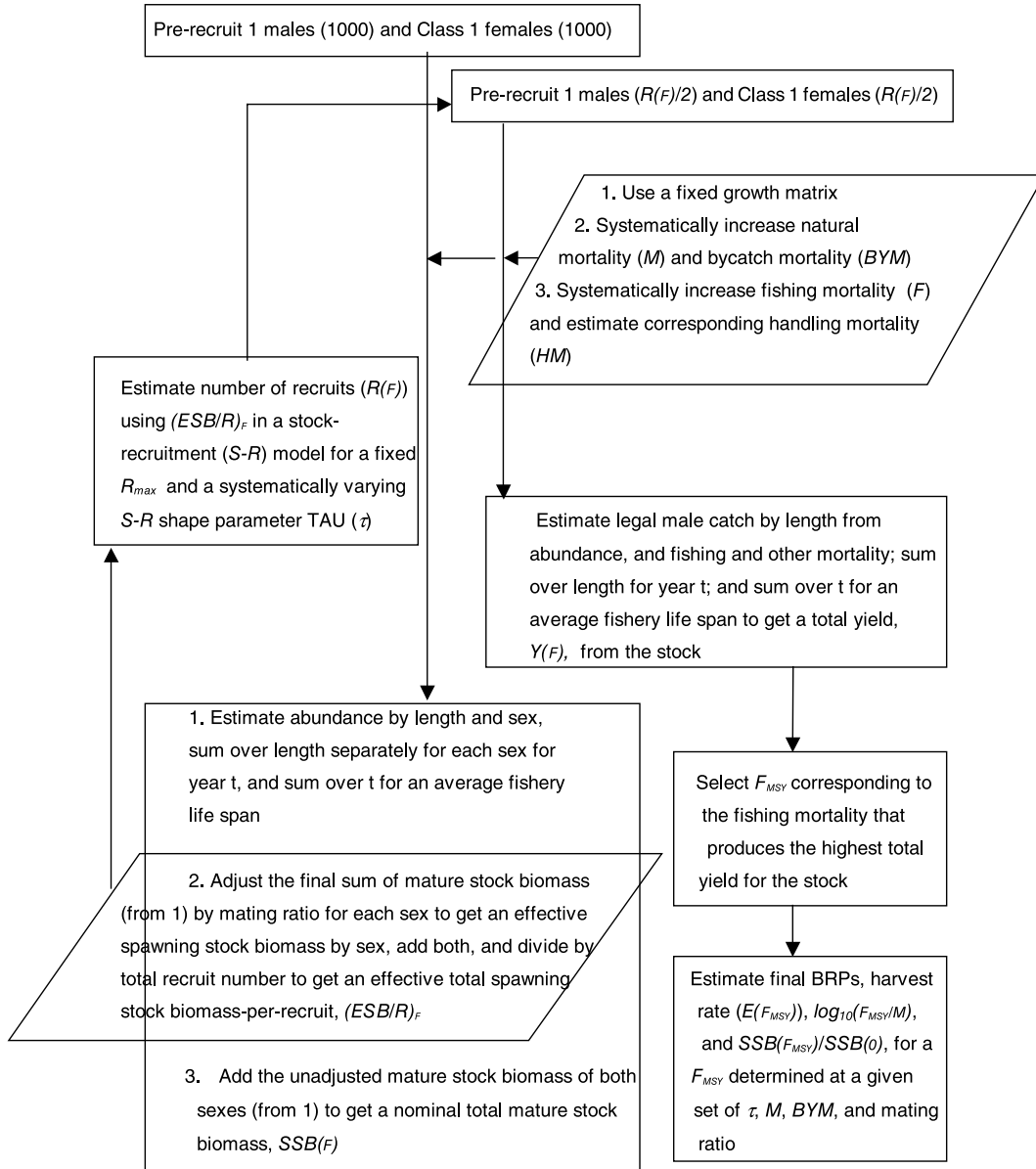$$\times e^{-MT}(1 - e^{-(F+(M+BYM)\delta)}) \tag{17}$$

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│ Pre-recruit 1 males (1000) and Class 1 females (1000) │
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Pre-recruit 1 males ($R(F)/2$) and Class 1 females ($R(F)/2$)

1. Use a fixed growth matrix
2. Systematically increase natural mortality (M) and bycatch mortality (BYM)
3. Systematically increase fishing mortality (F) and estimate corresponding handling mortality (HM)

Estimate number of recruits ($R(F)$) using $(ESB/R)_F$ in a stock-recruitment (S-R) model for a fixed R_{max} and a systematically varying S-R shape parameter TAU (τ)

Estimate legal male catch by length from abundance, and fishing and other mortality; sum over length for year t; and sum over t for an average fishery life span to get a total yield, $Y(F)$, from the stock

1. Estimate abundance by length and sex, sum over length separately for each sex for year t, and sum over t for an average fishery life span

2. Adjust the final sum of mature stock biomass (from 1) by mating ratio for each sex to get an effective spawning stock biomass by sex, add both, and divide by total recruit number to get an effective total spawning stock biomass-per-recruit, $(ESB/R)_F$

3. Add the unadjusted mature stock biomass of both sexes (from 1) to get a nominal total mature stock biomass, $SSB(F)$

Select F_{MSY} corresponding to the fishing mortality that produces the highest total yield for the stock

Estimate final BRPs, harvest rate ($E(F_{MSY})$), $log_{10}(F_{MSY}/M)$, and $SSB(F_{MSY})/SSB(0)$, for a F_{MSY} determined at a given set of τ, M, BYM, and mating ratio

Fig. 1. Flow chart of steps to determine harvest rate and biomass-based biological reference points by the length-based per-recruit model (see Appendix B for the formulae).

The total legal male catch ($C(F)$ and $Y(F)$) for the average fishery life span of the cohort was obtained by

$$C(F) = \sum_{t=t_r}^{\lambda} c(F)_t \tag{18}$$

$$Y(F) = \sum_{t=t_r}^{\lambda} y(F)_t \tag{19}$$

The F_{MSY} for a given set of growth and other mortality parameters (natural mortality, sublegal crab handling mortality, and bycatch mortality) was determined by

Table 1
Formulas to estimate $R(F)$, $ESB(F)$ and various proportions from $(ESB/R)_F$ for BRP determination[a]

Beverton and Holt S–R model		Ricker S–R model	
$R(F) = \dfrac{(ESB/R)_F - \alpha}{\beta(ESB/R)_F}$	(8)	$R(F) = \dfrac{\ln(\gamma(ESB/R)_F)}{\theta(ESB/R)_F}$	(9)
$ESB(F) = \dfrac{(ESB/R)_F - \alpha}{\beta}$	(10)	$ESB(F) = \dfrac{\ln(\gamma(ESB/R)_F)}{\theta}$	(11)
$X = \dfrac{((ESB/R)_{F=F_{MSY}} - \alpha)}{((ESB/R)_{F=0} - \alpha)}$	(12)	$X = \dfrac{\ln(\gamma(ESB/R)_{F=F_{MSY}})}{\ln(\gamma(ESB/R)_{F=0})}$	(13)
$\dfrac{R(F_{MSY})}{R(0)} = \dfrac{((ESB/R)_{F=F_{MSY}} - \alpha)(ESB/R)_{F=0}}{((ESB/R)_{F=0} - \alpha)(ESB/R)_{F=F_{MSY}}}$	(14)	$\dfrac{R(F_{MSY})}{R(0)} = \dfrac{\ln(\gamma(ESB/R)_{F=F_{MSY}})(ESB/R)_{F=0}}{\ln(\gamma(ESB/R)_{F=0})(ESB/R)_{F=F_{MSY}}}$	(15)

[a] The formulas are listed separately for Beverton and Holt, and Ricker stock–recruitment (S–R) models. ($ESB(F)$: effective total spawning stock biomass corresponding to a fishing mortality F; $R(F)$: number of recruits produced by $ESB(F)$; $(ESB/R)_F$: effective total spawning stock biomass-per-recruit corresponding to F; F_{MSY}: MSY-producing fishing mortality; $\alpha, \beta, \gamma, \theta$: parameters of S–R models).

systematically searching for a maximum $Y(F)$ over F from 0.01 to 10 in 0.01 increments. The mean crab weight at F_{MSY}, $W(F_{MSY})$, was determined by $Y(F)/C(F)$ at F_{MSY}. The $W(0)$ was determined at F closer to zero (0.01). The $E(F_{MSY})$ was determined using Eq. (2) at F_{MSY}.

The biomass-based BRP was determined in terms of nominal $SSB(F)$ because it could be related to survey estimates of biomass for monitoring purposes. The $SSB(F)$ was estimated as the sum of male and female total mean spawning stock biomass generated from 1000 pre-recruit 1 male and 1000 class 1 female crabs without adjusting for mating ratio. It was calculated using Eqs. (B.16)-(B.21) ignoring the "effective MSSN(F)/MSSN(F)" and "effective FSSN(0)/FSSN(0)" terms. Thus, this $SSB(F)$ was the unconstrained (or nominal) total mature stock biomass, part or whole of which produced $R(F)$ for $Y(F)$ estimation.

The simulations were performed by VBA programming (Walkenbach, 1999). The $E(F_{MSY})$, $\log_{10}(F_{MSY}/M)$, and $SSB(F_{MSY})/SSB(0)$ were plotted against τ for various plausible combinations of M, h, and BYM. The F_{MSY}/M ratio was expressed in $\log_{10}$ form to be comparable with other BRPs in the figures because this ratio exceeded 1 in most cases.

2.3. Bristol Bay red king crab biological and fisheries parameters used in the simulations

The Bristol Bay red king crab sizes (in mm CL) were grouped into 5 mm intervals. Following Collie and Kruse (1998), Zheng et al. (1995a) and Kruse et al. (2000), the pre-recruit 1 crabs were those in the 120–134 mm CL size range (three 5 mm size intervals); recruit and post-recruit crabs were in the 135–169 mm CL size range (seven 5 mm size intervals). Pre-recruit 1 crabs were approximately one moult growth increment smaller than the recruits and were mature (Paul and Paul, 1990; Zheng et al., 1995a; Kruse et al., 2000). The mature female size range was arbitrarily divided into two classes: class 1, 90–99 mm CL (two 5 mm size intervals); and class 2, 100–139 mm CL (eight 5 mm size intervals). Approximately 50% of females mature by 89 mm CL and 80% by 95 mm CL (Otto et al., 1990); therefore, 90 mm CL was chosen as the knife-edge female maturity length.

The male-only crab fishery management strategy requires any female catch to be immediately returned to sea. Thus, the male pre-recruit 1 stage and the two classes of females suffered M, HM and BYM; whereas, male fishery recruit and post-recruit stages suffered F, M and BYM. For simplicity, these parameters were kept constant and equal among all stages, but varied to different levels at each simulation. The parameters required for the length-based analysis are listed in Table 2.

The τ was varied from 0.05 to 0.75 by 0.05 increments to provide varied steepness near the origin and overall shape to the two S–R curves. A narrow range of 0.05–0.5 was adequate for crabs because it covered values from a high compensation level of 0.05 (survival at low stock sizes approximately 20 times that at the virgin size) to a low compensation level of 0.5

Table 2
Bristol Bay red king crab parameter values used in the simulations[a]

Parameter	Male	Female	Remarks
Growth increment model (Eq. (B.8))			
$\bar{l}$	16.0 mm CL	4.0 mm CL	Weber and Miyahara (1962) for males, Gray (1963) for females
s	2.4 mm CL	0.6 mm CL	Assumed 15% CV
Molt probability model (Eq. (B.9))			
g	295159.6		Medium growth period (1985–1991); Zheng et al. (1995b)
d	0.089		
Molt probability		1.0	Zheng et al. (1995a)
Weight–length model (g mm CL) (Eq. (B.23))			
a	0.0003614	0.02286	Balsiger (1974) for males, Zheng et al. (1995a) for females
b	3.16	2.234	

[a] CV: coefficient of variation; CL: carapace length.

(survival at low stock sizes about twice that at the virgin size). The complex mating behaviour, the success of which depends on the sex ratio, distribution and size differences (Kruse, 1993; Zheng et al., 1995a), and prolonged poor recruitment of many Alaskan crabs suggests that τ value would fall at higher values of this narrow range. Although τ values above 0.5 are possible, they are likely to be rare because for those values the survival at low stock levels would approach or go below that at the virgin size, which is very unlikely under normal environmental conditions. Note that Mace (1994) identified the 0.05–0.5 range as suitable for many fish populations.

The male to female mean mating ratio was set at 1:1, 1:2 and 1:3. Based on a laboratory study, Paul and Paul (1997) suggested a likely average mating ratio of one legal-sized male to three multiparous females for population modelling purposes. An earlier laboratory study by the same authors suggested lower mating ratios for smaller sized males (Paul and Paul, 1990). Thus, the average ratios considered here would adequately capture the size-specific variation in mating ratios of red king crabs.

The M was varied from 0.2 to 0.4 by 0.1 increments. The BSAI crab fisheries management guidelines (NPFMC, 1999) specified an M of 0.2 for king crabs. This was based on the maximum life expectancy of king crabs, which could range from 21 to 24 years (Matsuura and Takeshita, 1990; Stevens et al., 2000a). However, in recent studies, an M of 0.3 has been considered appropriate for the male Bristol Bay red king crab stock (Kruse et al., 2000). The M range con-

sidered for the simulations took care of this value as well. The *HM* was related to legal crab *F* (Eq. (B.7)) with the assumption that the catchability of sublegal crabs was half of that of the legal crabs (Zheng et al., 1997a) and there was 20% mortality (an *h* of 0.2) on captured and subsequently released sublegal male and female crabs (Kruse et al., 2000). The *h* was varied at two levels, 0 and 0.2, to obtain 0 and 20% mortality due to handling, which was converted to an instantaneous handling mortality, *HM*, using Eq. (B.7). The *BYM* was also varied at two levels, 0 and 0.01. Based on 1994–1999 bycatch weighted (by stock size) average harvest rates from all fisheries (NPFMC, 2000), a maximum *BYM* of 0.01 was estimated.

The actual size distributions of pre-recruit 1 males and class 1 females are not well known. Therefore, the initial number of individuals (i.e., total pre-recruit 1 and class 1 crabs) was equally distributed among the 5 mm CL size intervals within each stage. However, the subsequent growth increment at each moult was assumed to be normal with a constant mean and a standard deviation (Table 2) to determine growth proportion ($P_{l',l}$). There was no unique age for the initial stage because it was comprised of various ages depending on individual growth histories (Stevens, 1990). Hence, a relative age of zero ($t_r = 0$) for the entire size range of pre-recruit 1 and class 1 was assumed and kept track of the male and female cohorts for 10 years ($\lambda = 10$). Bristol Bay red king crab recruit to the fishery 7–12 years after hatching (Kruse et al., 2000) and females of average size 97 mm CL were about 6 years old (Zheng et al., 1995a). Therefore, a

reasonable guess for the minimum age of pre-recruit 1 males and class 1 females would be 6 years. So, after 10 years, the cohort age would be 16 years at the minimum. Although the maximum life expectancy of red king crab is over 20 years, very few crabs live longer than 15 years (Alverson, 1980; Kruse et al., 2000). Hence tracking the cohort for 10 years for BRP estimation is reasonable.

The mean estimate of δ for the 1996–2000 fishing seasons (ADF&G, 2001) was 0.0121 year. The mean value of T for the 1995–1999 fishing seasons was 0.3836 year (various AFSC processed reports by NMFS, Kodiak). The δ was used in generating both abundance and catch from males, whereas T was used only to generate male catch.

3. Results

3.1. F_{MSY} to M relationship

F_{MSY} is equal to M when the terms inside the brackets on the right-hand side of Eq. (1) reduce to one for some input values. This occurred only for limited cases for the Bristol Bay red king crab stock considered in this paper (see Figs. 2–7). Eq. (1) was also used to confirm the F_{MSY} estimates obtained by the systematic search method. This was possible because $R(F_{MSY})/R(0)$, $W(F_{MSY})/W(0)$ and X ratios could be determined at F_{MSY} during the simulation process. Eq. (1) was solved for F_{MSY} by a nonlinear method using the EXCEL2000 solver routine. The F_{MSY} estimates obtained by Eq. (1) and the search method were close, confirming that the search method produced acceptable values of F_{MSY}.

3.2. F_{MSY}, $E(F_{MSY})$, and SSB(F_{MSY})/SSB(0) determination

3.2.1. Beverton and Holt S–R model

The $\log_{10}(F_{MSY}/M)$ and $E(F_{MSY})$ steadily decreased with increasing τ (Figs. 2–4). The F_{MSY} exceeded M for most of the scenarios except the 1:1 mating ratio (Figs. 2–4). Even at that ratio, F_{MSY} was equal to or less than M only at higher τ values, exceeding 0.35. The F_{MSY} converged below the maximum $F = 10$ set for the search. The handling mortality had more influence on the trends of the

curves than *BYM* (compare Figs. 2–4). As τ increased, the SSB(F_{MSY})/SSB(0) ratio steadily increased from 0.37 to 0.9 with a median of 0.53 for all combinations of mortality and mating ratio (Table 3). Fig. 4 depicts the trends in BRP ratios for more likely values of handling mortality ($h = 0.2$) and bycatch mortality (*BYM* = 0.01). For most likely values of $M = 0.3$, $h = 0.2$, *BYM* = 0.01, and τ range = 0.3–0.5, the median SSB(F_{MSY})/SSB(0) ratios were 0.69 and 0.5 for the mating ratios 1:1 and 1:3, respectively (Table 3). Thus, the median total mature stock biomass at the MSY-producing level was about 50–69% of the virgin biomass. For the same scenario, the median $E(F_{MSY})$ values were 0.21 and 0.50 for mating ratios 1:1 and 1:3, respectively (Table 3).

3.2.2. Ricker S–R model

The trends in $\log_{10}(F_{MSY}/M)$, $E(F_{MSY})$, and SSB(F_{MSY})/SSB(0) with increasing τ were similar to that observed under the Beverton and Holt S–R model except those for the first two at small τ values (Figs. 5–7). For most cases, F_{MSY} converged below the maximum $F = 10$ set for the search. However, when mating ratio > 1:1, the $\log_{10}(F_{MSY}/M)$ and $E(F_{MSY})$ curves flattened at low τ values for all combinations of *HM* and *BYM* as M and mating ratio increased because $Y(F)$ was ever increasing and the search converged to the maximum F value (hence $E(F_{MSY})$ reached nearly 1) (Figs. 5–7). The SSB(F_{MSY})/SSB(0) declined initially and steadily increased as τ increased. The $\log_{10}(F_{MSY}/M)$ and $E(F_{MSY})$ decreases were sharp at higher τ values. The F_{MSY} exceeded M for most of the scenarios except the 1:1 mating ratio. Even at that ratio, F_{MSY} was equal to or less than M only at τ values exceeding 0.4. The SSB(F_{MSY})/SSB(0) ratio ranged from 0.27 to 0.89 with a median of 0.51 for all combinations of mortality and mating ratio (Table 3). The large SSB(F_{MSY})/SSB(0) ratios occurred at higher τ values, which were very unlikely for the Bristol Bay red king crab stock. The handling mortality had more influence on the decline of the curves than the bycatch mortality (Figs. 5–7). For the more likely scenario $M = 0.3$, $h = 0.2$, *BYM* = 0.01 and τ range = 0.3–0.5, the median SSB(F_{MSY})/SSB(0) values were 0.66 and 0.46 at mating ratios 1:1 and 1:3, respectively (Table 3); thus, the median total mature stock biomass at the MSY-producing level was about 46–66% of the virgin biomass. Under the same set
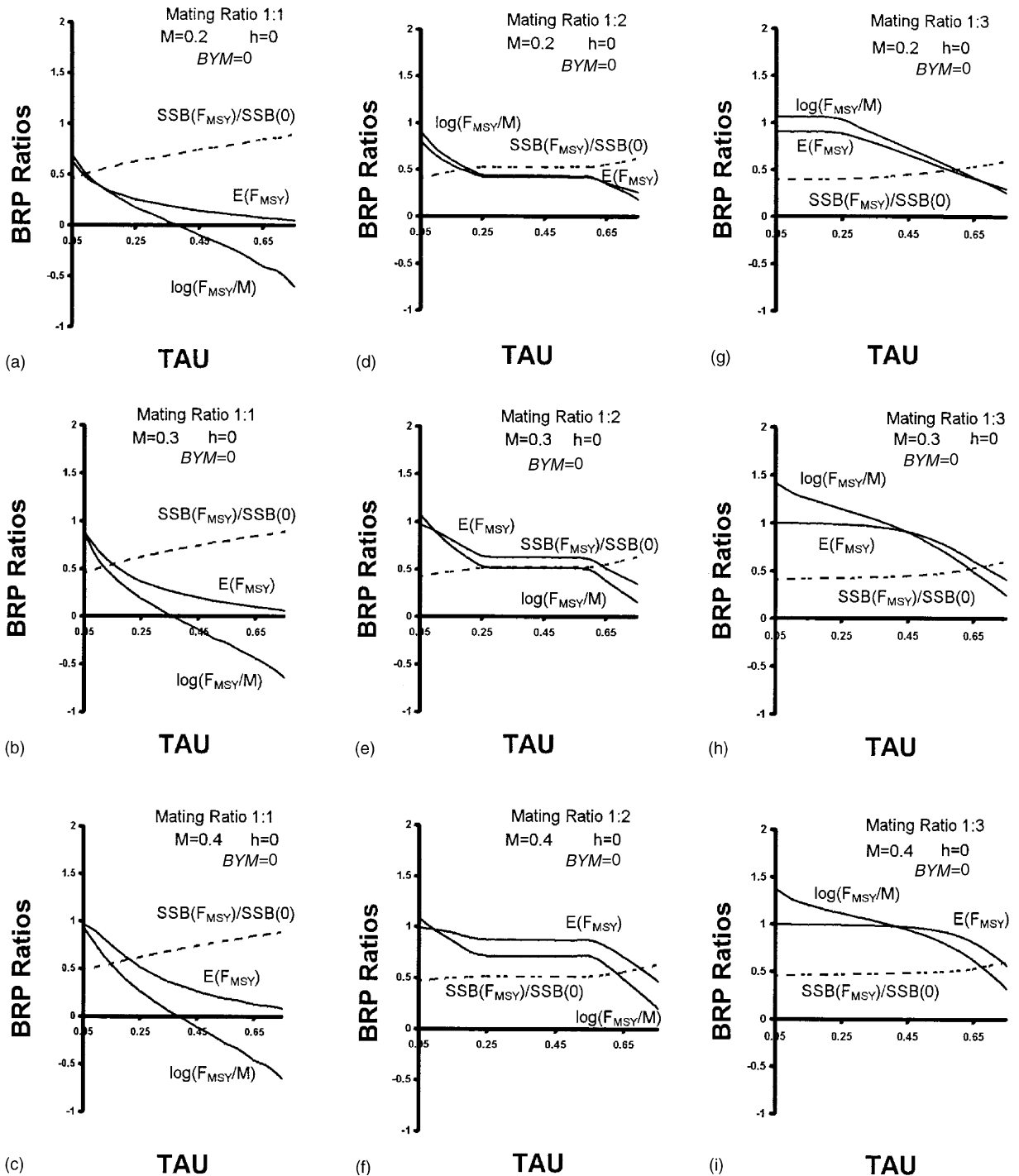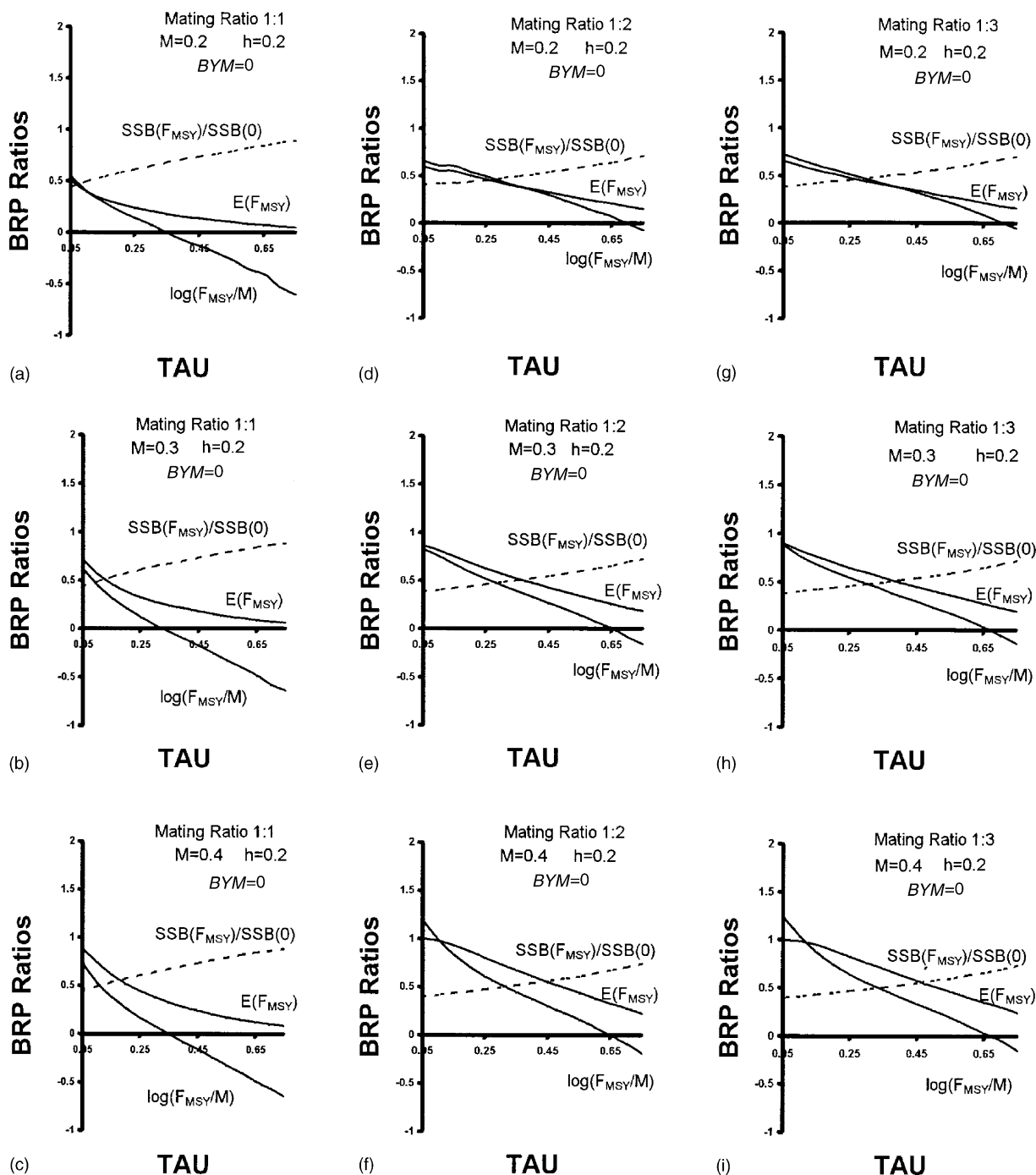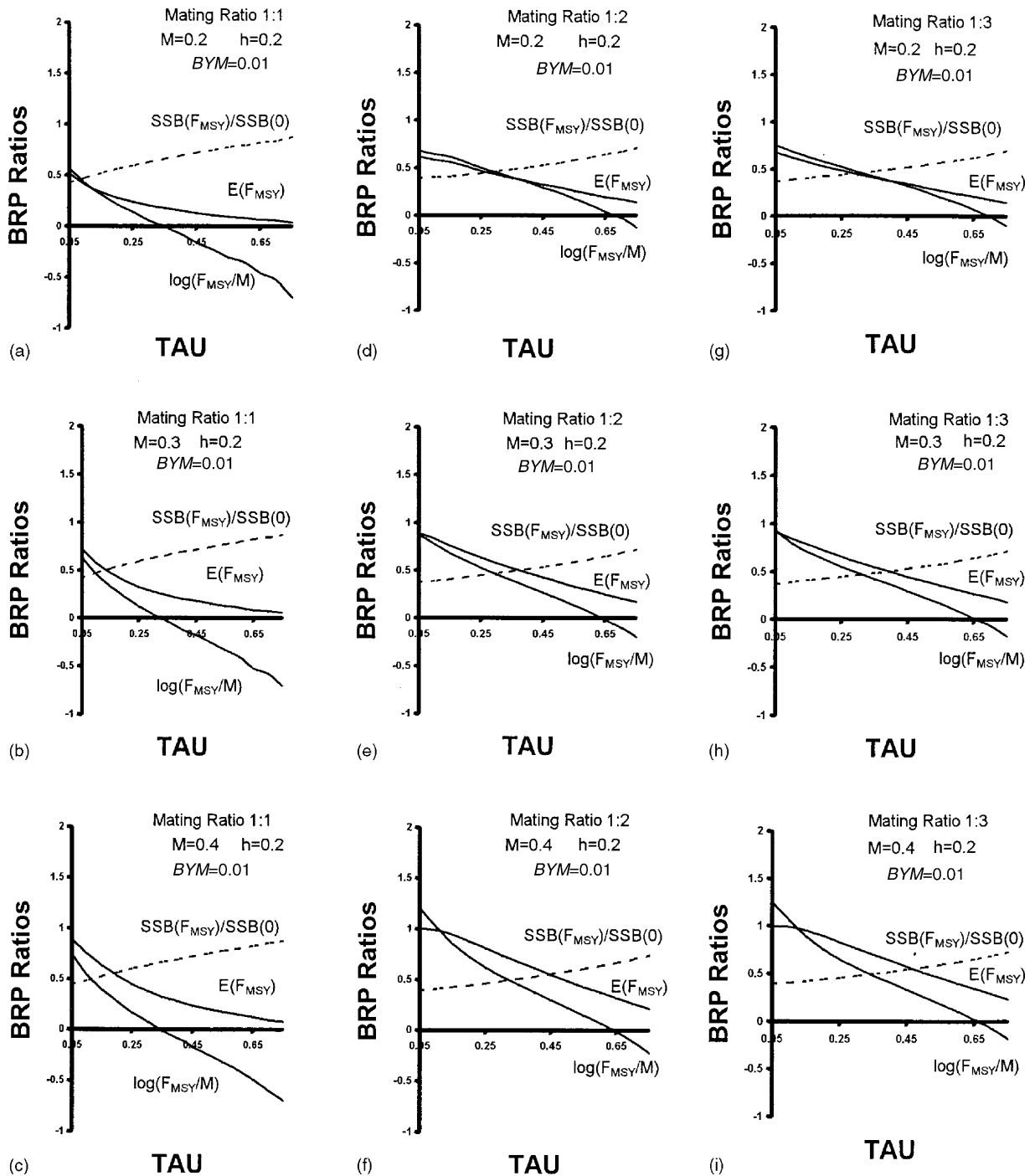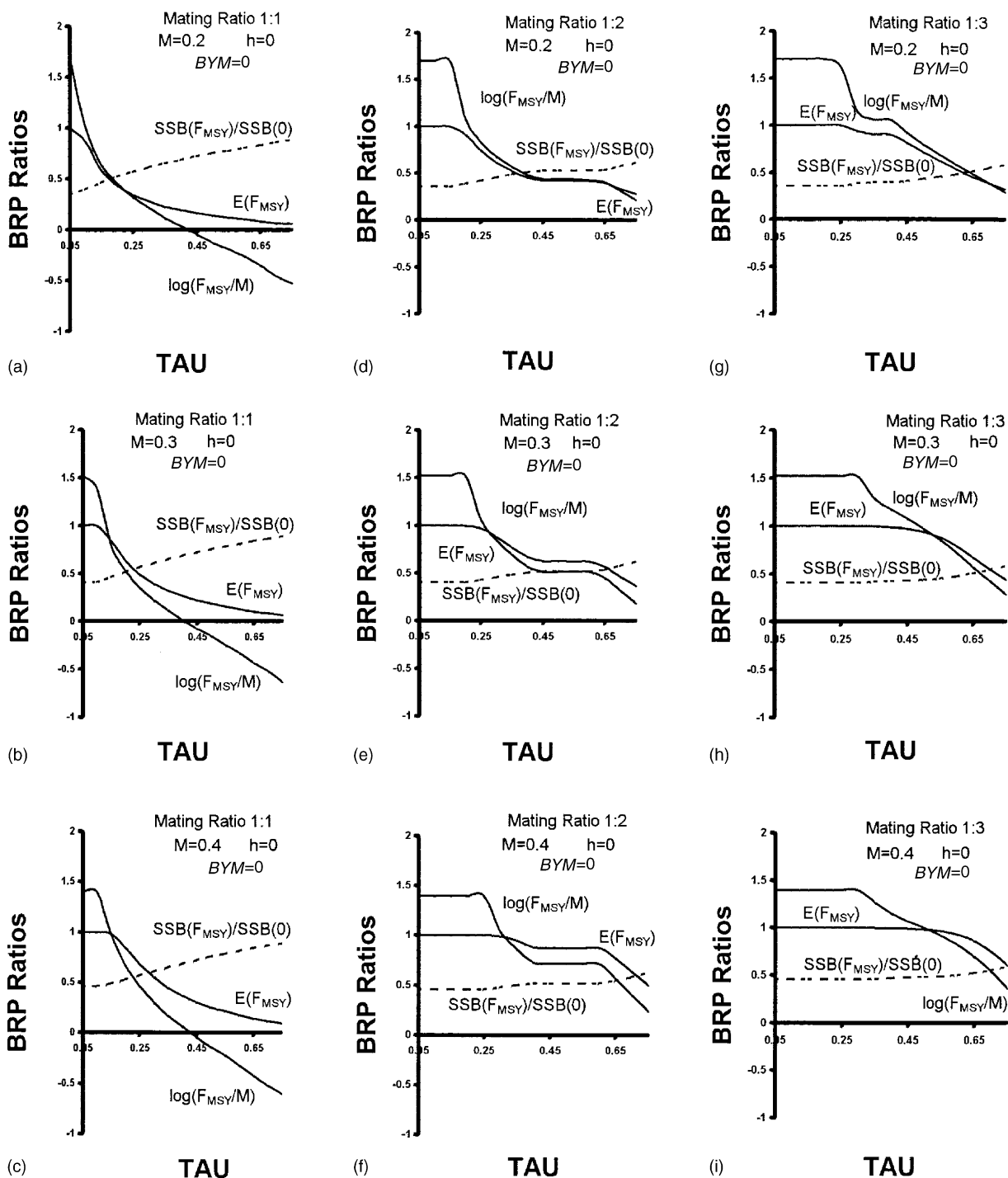
Fig. 2. Effects of various combinations of M, mating ratio and Tau (τ) on estimates of equilibrium $\log_{10}(F_{MSY}/M)$ (solid line), $E(F_{MSY})$ (solid line) and SSB(F_{MSY})/SSB(0) (dotted line) for Bristol Bay red king crab for the Beverton and Holt S–R model under no handling ($h = 0$) and bycatch ($BYM = 0$) mortality.
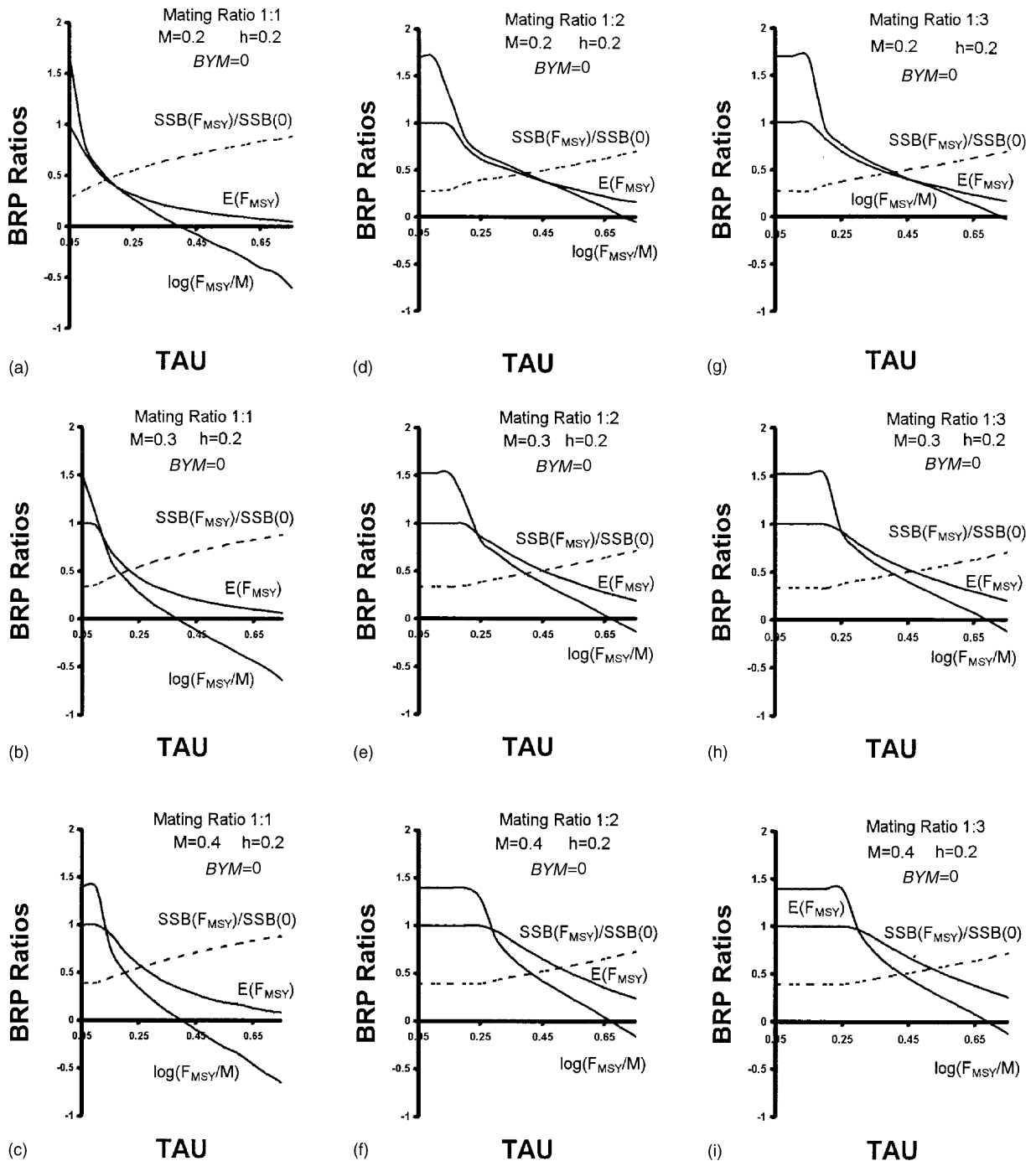
Fig. 3. Effects of various combinations of M, mating ratio and Tau (τ) on estimates of equilibrium $\log_{10}(F_{MSY}/M)$ (solid line), $E(F_{MSY})$ (solid line), and $SSB(F_{MSY})/SSB(0)$ (dotted line) for Bristol Bay red king crab for the Beverton and Holt S–R model under a plausible fixed value of handling mortality ($h = 0.2$), but no bycatch mortality ($BYM = 0$).
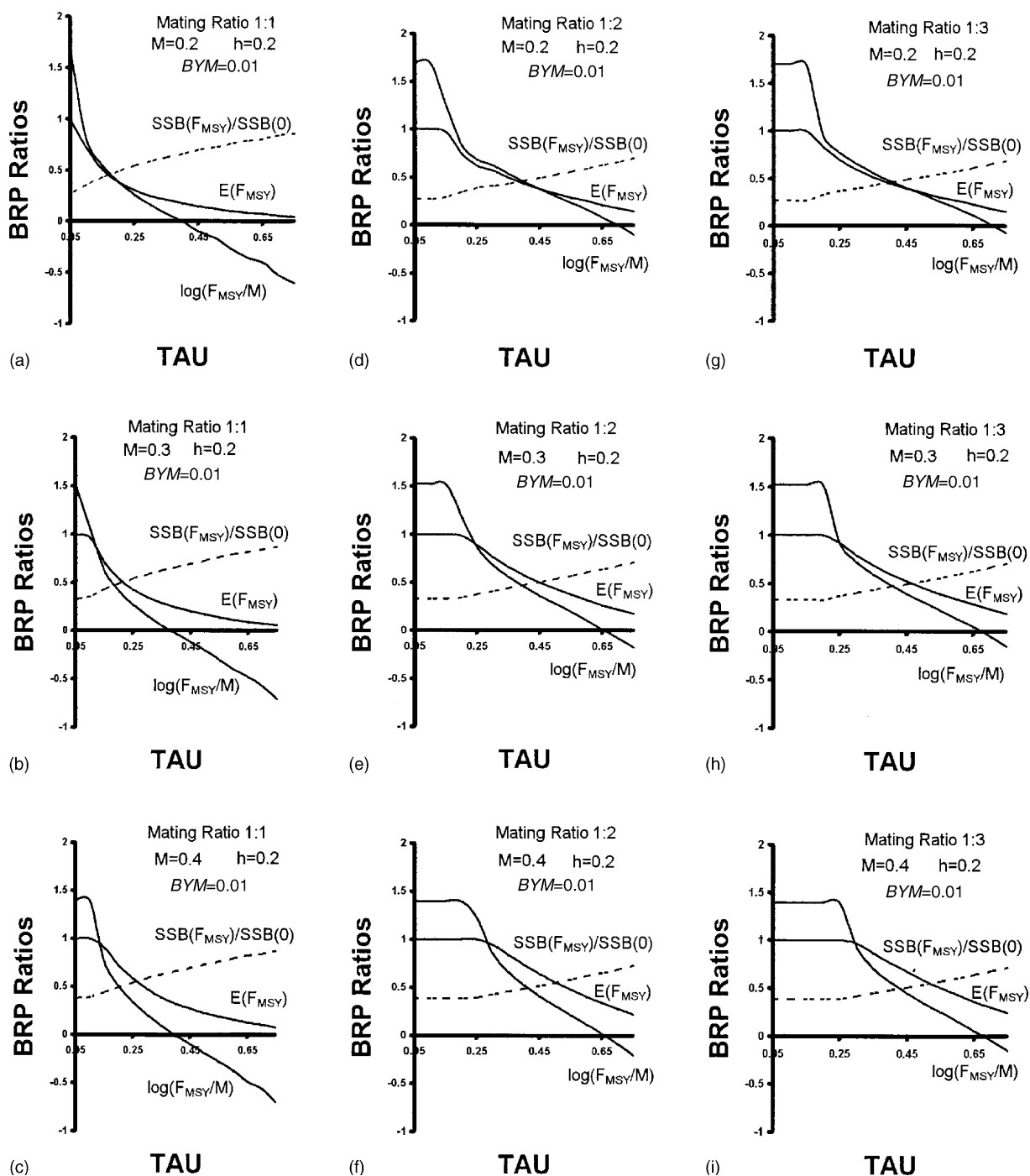
Fig. 4. Effects of various combinations of M, mating ratio and Tau (τ) on estimates of equilibrium $\log_{10}(F_{MSY}/M)$ (solid line), $E(F_{MSY})$ (solid line) and SSB(F_{MSY})/SSB(0) (dotted line) for Bristol Bay red king crab for the Beverton and Holt S–R model under plausible fixed values of handling ($h = 0.2$) and bycatch ($BYM = 0.01$) mortality.

Fig. 5. Effects of various combinations of M, mating ratio and Tau (τ) on estimates of equilibrium $\log_{10}(F_{MSY}/M)$ (solid line), $E(F_{MSY})$ (solid line) and SSB(F_{MSY})/SSB(0) (dotted line) for Bristol Bay red king crab for the Ricker S–R model under no handling ($h = 0$) and bycatch ($BYM = 0$) mortality.

Fig. 6. Effects of various combinations of M, mating ratio and Tau (τ) on estimates of equilibrium $\log_{10}(F_{MSY}/M)$ (solid line), $E(F_{MSY})$ (solid line) and SSB(F_{MSY})/SSB(0) (dotted line) for Bristol Bay red king crab for the Ricker S–R model under a plausible fixed value of handling mortality ($h = 0.2$), but no bycatch mortality ($BYM = 0$).

Fig. 7. Effects of various combinations of M, mating ratio and Tau (τ) on estimates of equilibrium $\log_{10}(F_{MSY}/M)$ (solid line), $E(F_{MSY})$ (solid line) and SSB(F_{MSY})/SSB(0) (dotted line) for Bristol Bay red king crab for the Ricker S–R model under plausible fixed values of handling ($h = 0.2$) and bycatch ($BYM = 0.01$) mortality.

Table 3

Estimates of maximum sustainable yield (MSY)-producing total mature biomass as a proportion of virgin total mature biomass (SSB(F_{MSY})/SSB(0)) and MSY-producing legal male harvest rate at the time of the fishery ($E(F_{MSY})$) for Beverton and Holt, and Ricker stock–recruitment (S–R) models for Bristol Bay red king crab[a]

Input parameter range					Estimated biological reference points			
Mortality	Mating ratio	τ			Beverton and Holt S–R		Ricker S–R	
					Range	Median	Range	Median
$M = 0.2, 0.3, 0.4$; $h = 0, 0.2$; $BYM = 0, 0.01$	1:1; 1:2; 1:3	0.05–0.75	SSB(F_{MSY})/SSB(0), $E(F_{MSY})$		0.37–0.90, 0.04–1.00	0.53, 0.46	0.27–0.89, 0.05–1.00	0.51, 0.59
$M = 0.2, 0.3$; $h = 0.2$; $BYM = 0.01$	1:1; 1:2; 1:3	0.3–0.5	SSB(F_{MSY})/SSB(0) $E(F_{MSY})$		0.46–0.75, 0.11–0.77	0.54, 0.39	0.40–0.73, 0.13–0.97	0.51, 0.47
$M = 0.3$; $h = 0.2$; $BYM = 0.01$	1:1; 1:2; 1:3	0.3–0.5	SSB(F_{MSY})/SSB(0), $E(F_{MSY})$		0.46–0.74, 0.16–0.60	0.54, 0.43	0.40–0.73, 0.17–0.79	0.50, 0.50
$M = 0.3$; $h = 0.2$; $BYM = 0.01$	1:1	0.3–0.5	SSB(F_{MSY})/SSB(0), $E(F_{MSY})$		0.63–0.74, 0.16–0.28	0.69, 0.21	0.58–0.73, 0.17–0.35	0.66, 0.24
$M = 0.3$; $h = 0.2$; $BYM = 0.01$	1:3	0.3–0.5	SSB(F_{MSY})/SSB(0), $E(F_{MSY})$		0.46–0.55, 0.40–0.60	0.50, 0.50	0.40–0.52, 0.46–0.79	0.46, 0.60

[a] M: annual instantaneous natural mortality; h: handling mortality proportion of sublegal males and all females caught by fishing and released; BYM: annual instantaneous bycatch mortality. Mating ratio: number of females mated by one male in one spawning occasion; τ: extinction parameter defining the steepness near the origin and overall shape of the S–R curve.

of conditions, the median $E(F_{MSY})$ values were 0.24 and 0.60 at mating ratios 1:1 and 1:3, respectively (Table 3).

In summary, for both types of S–R models, higher mating ratios resulted in higher threshold harvest rates, but lower threshold mature stock biomass ratios. The median MSY-producing mature stock biomass was closer to or above half of the virgin mature stock biomass at more likely τ and mating ratio values (Table 3).

4. Discussion

The F_{MSY} formula as a function of M established in this paper was based on a general, age-specific cohort growth (in weight) model incorporated into an age-specific cohort survival model (Beverton and Holt, 1957). This equation was applicable to any fisheries resource and was applied to Bristol Bay red king crabs with parameters estimated by the length-based method. The results suggested F_{MSY} to be higher than M under a number of feasible conditions and less than or equal to M for a few restricted conditions when the mating ratio was 1:1 and the τ value was high.

A number of investigations based on teleost fish population parameters concluded M to be an upper limit for F_{MSY} (e.g., Deriso, 1982; Quinn and Deriso, 1999). This was not the general case for the red king crab stock. Differences in growth pattern and mating behaviour and the single-sex exploitation strategy have made crab stock dynamics quite different from that of teleosts, and one should be cautious when selecting the same teleost-based BRP values to formulate crab-harvesting strategies. Thompson (1992), considering a family of dynamic pool models, showed that Alverson and Pereyra's (1969) two rules of thumb used in fisheries management, $F_{MSY} = M$ and $SSB(F_{MSY}) = 0.5\,SSB(0)$, could not be satisfied simultaneously under certain S–R and weight-at-age relationships, and concluded that F_{MSY} could be higher or lower than M depending on the shape of the S–R curve. Most of his statement was valid for the red king crab stock as well, except for the last portion. It was not only the shape of S–R curves but also the mating behaviour, which defines $ESB(F)$, and the growth pattern that changed the F_{MSY} to M relation in the direction of $F_{MSY} > M$, for a number

of feasible scenarios considered for the red king crab stock.

Reasonably close estimates of F_{MSY} (equivalently legal male harvest rate $E(F_{MSY})$) and mature stock biomass at $F_{MSY}(SSB(F_{MSY}))$ for a stock would be ideal to formulate an optimum harvesting strategy. If an S–R relationship, growth increment, moulting probability, natural mortality, handling mortality and bycatch mortality were known, this could be achieved. The exact S–R model could be used in the simulation to determine $E(F_{MSY})$ and $SSB(F_{MSY})/SSB(0)$ ratios. The latter, along with an estimate of maximum $SSB(F)$ (or a median or a mean value from a certain number of large $SSB(F)$ estimates) during a given environmental period, could be used to estimate $SSB(F_{MSY})$. However, most stocks lack necessary biological and fisheries information to establish an S–R relationship. This was the case for a number of crab stocks in the BSAI. The best option under this circumstance was to consider a few well-known S–R models with a narrow, but appropriate, variation in τ to obtain a plausible range of shapes of S–R curves, to get a reasonably narrow range of $E(F_{MSY})$ and $SSB(F_{MSY})/SSB(0)$ ratios. Thus, the length-based simulations considered two well-known S–R models: Beverton and Holt, and Ricker with a τ range = 0.05–0.75 for investigating the trends in $\log_{10}(F_{MSY}/M)$, $E(F_{MSY})$, and $SSB(F_{MSY})/SSB(0)$. A still narrower, but plausible, τ range = 0.3–0.5 was considered to estimate narrow ranges of $E(F_{MSY})$ and $SSB(F_{MSY})/SSB(0)$ ratios. A number of king crabs in the BSAI were in depressed stock status for a long period of time (ADF&G, 2001) and it is prudent to consider them to be less resilient to overexploitation. Thus, the choice of the τ range of 0.3–0.5 was appropriate. Note that the lower limit, 0.3, was suggested as an appropriate default overfishing threshold value for little-known stocks by Mace and Sissenwine (1993). Although the τ range for exploration was directly borrowed from a teleost-type modelling investigation by Mace (1994), it covered a reasonably wide range of steepness (and shape) of the Beverton and Holt, and Ricker S–R curves that could be expected in a crab S–R relationship.

The major feature of the BSAI crab-harvest strategy was the formulation of a GHL. This was calculated by multiplying the mature male biomass by a predetermined harvest rate (Kruse et al., 2000). Therefore, $E(F_{MSY})$ (harvest rate) was a more useful

parameter to focus on than F_{MSY}. According to the Magnuson–Stevens Fishery Conservation and Management Act, the $E(F_{MSY})$ was a limit reference point. Consequently, the selected $E(F_{MSY})$ ranges should be treated as upper limits, and the target harvest rates should be set at lower levels to provide a buffer against overshooting $E(F_{MSY})$, perhaps at 75% of the $E(F_{MSY})$ when the stocks are near or above the MSY-producing levels, and reduced further by a proportion of current stock biomass over MSY-producing stock biomass when they are below MSY-producing levels (Restrepo and Powers, 1999). This procedure was followed in some BSAI crab rebuilding plans (e.g., snow crab rebuilding strategy (Zheng et al., 2002)). Note that the 25% reduction in the harvest rate was sufficient or not dependent on a number of factors, particularly on uncertainty in assessment (Restrepo and Powers, 1999). The $E(F_{MSY})$ and SSB(F_{MSY})/SSB(0) varied with increasing M and τ at a given mating ratio at plausible HM and BYM values for both types of S–R models (Figs. 4 and 7). Consequently, a narrow τ range was required to estimate plausible $E(F_{MSY})$ and SSB(F_{MSY})/SSB(0) ranges for a more likely set of M, HM, BYM, and mating ratio values.

The Bristol Bay red king crab fishery is cooperatively managed by the State of Alaska and the US Federal government to achieve two primary objectives: (1) ensure adequate spawning biomass for sufficient recruitment, and (2) achieve optimum yield over the long term with minimum variability (Zheng et al., 1997a). Two sets of reference points, one by the Federal and the other by the state, are jointly used to manage the fishery to meet the objectives. The Federal reference points are: (1) an MSST threshold of 20 300 t below which the stock is declared "overfished," and (2) a maximum harvest rate of 20% above which the stock is declared "overfishing, whereas the state reference points, since 1996, are: (1) 8.4 millions of mature females and 6600 t of effective spawning stock biomass (of females) as thresholds, (2) 10% harvest rate when the stock is above the thresholds, but the effective spawning stock biomass is below 25 000 t (the target stock rebuilding level, an intermediate level of biomass above which strong recruitment occurred with a high frequency in the past (Zheng et al., 1997b)), or 15% when the stock is above the thresholds and the effective spawning stock biomass is above 25 000 t, (3) a

50% cap on legal male harvest, and (4) a minimum of 1800 t GHL for a fishery to open. The fishery will be closed when the stock is below the thresholds, which are set to prevent recruitment overfishing. The percentage harvest cap is set to prevent over harvesting of legal males (Pengilly and Schmidt, 1995). The lower harvest rate is set by the state following a simulation study, which proposed a robust harvest strategy under uncertainties of recruitment and high natural and handling mortality that a combination of a 15% mature male harvest rate, a 50% cap on legal male harvest, and a threshold level of 11 000 t (25% of the pristine effective (female) spawning stock biomass, an MSST proxy) produced a high mean yield with low variability while protecting crab reproductive potential (Zheng et al., 1997a). However, the 11 000 t threshold level has not been used, instead the lower threshold value of 6600 t (∼8.4 million mature females) is preferred. The latter was determined, following Thompson's rule (NPFMC, 1990; Thompson, 1993), as 20% equilibrium spawning stock as estimated from the Ricker S–R model.

Additional management practices include sex–size–season restrictions and effort limitation through vessel registration, pot limits and other gear restrictions (ADF&G, 1999). Some results (Table 3) from the current simulation analysis could favourably be compared with Zheng et al.'s (1997a,b) findings even though the definitions of effective spawning stock biomass and optimum biomass differed between the two. Zheng et al. (1997b) used a general Ricker S–R model and their target biomass estimate was approximately 57% of the pristine biomass. In the current simulations, for possible ranges of values of τ (0.05–0.75), M (0.2, 0.3, 0.4), h (0, 0.2), BYM (0, 0.01), and mating ratio (1:1, 1:2, 1:3), the MSY-producing biomass varied from 27 to 89% of the pristine biomass with a median 51% and the threshold legal male harvest rate at the time of the fishery varied from 5 to 100% with a median 59% under the Ricker S–R model assumption. The median maximum target harvest rate of legal males at the time of the fishery (75% of the threshold) was 44%. On the other hand, when plausible ranges of values of τ (0.3–0.5), M (0.3), h (0.2) and BYM (0.01) were selected, the MSY-producing biomass varied from 58 to 73% of the pristine biomass with a median 66% and the threshold legal male harvest rate at the time of the fishery varied from 17 to 35% with a median 24% for

a mating ratio of 1:1. The corresponding median maximum target harvest rate of legal males at the time of the fishery was 18%. For a higher mating ratio of 1:3, the MSY-producing biomasses as a percentage of the pristine biomass were lower (with a median 46%) and the legal male harvest rates at the time of the fishery were higher (with a median 60%) for the same set of other parameter values (Table 3). Thus, although Zheng et al.'s (1997a,b) definitions of effective spawning biomass and target optimum biomass were different, their robust harvest strategy recommendation on the mature male harvest rate at the survey time and the rebuilding target biomass level was comparable to median values estimated at the more conservative mating ratio (1:1). Zheng et al. (1997a) also noted that the optimum harvest rate was inversely related to handling mortality and Kruse et al. (2000) used a moderate handling mortality proportion of 0.2. The current study selected Kruse et al.'s choice as the plausible handling mortality value even though the true handling mortality is yet to be determined. Natural mortality can also vary inter-annually and frequency of poor recruitment is high (Zheng et al., 1997a,b) perhaps due to environmental effects. Under these uncertainties, it is prudent to follow a precautionary approach by selecting a low harvest rate below 18% to rebuild the stock, currently below optimum (Vining and Zheng, 2001), to a level equal to or above 66% of the pristine total mature stock biomass.

Besides examining the F_{MSY} to M relationship, this paper focused on developing methods to estimate currently identified BRPs for crab management, such as $E(F_{MSY})$ and $SSB(F_{MSY})$, based on crab biological and fisheries principles with the primary purpose of utilising them for poorly understood stocks. Although other per-recruit-based BRPs, such as $F_{30\% \ SSB/R}$ to $F_{60\% \ SSB/R}$ ($F_{\%SPR}$ is the F maintaining the exploited spawning stock biomass-per-recruit at a given percentage of the virgin spawning stock biomass-per-recruit), with higher percentages corresponding to stocks with less resilience to fishing or environmental pressure (Restrepo and Powers, 1999), or a traffic light approach (Caddy, 2002), where a basket of suitable threshold reference points is used to detect the danger (or red light) zone by accumulating bad points when the BRP is infringed, might be equally good or better for crab management, this paper did not attempt to identify them. Furthermore,

only the growth increment was modelled stochastically while the cohort decline model was treated deterministically with constant mortality. To improve the methods presented in this paper, future research could focus on adding stochastic components to the cohort decline part of the length-based models incorporating size and shell age-specific mortality. In the meantime, as Mace (1994) pointed out, the simple deterministic findings may be treated as the median or average of the stochastic results.

Appendix A. Derivation of F_{MSY} to M relationship[1]

The following assumptions were made in the derivation:

1. Constant instantaneous fishing (F) and natural (M) mortality over post-recruit ages.
2. Knife-edge selection occurs, once per year, at the recruitment age, t_r, and the age-at-first-capture is equal to the age-at-recruitment.
3. Weight at any age, w_t, is invariant of the size at that age.
4. The stock is in a steady state determined by F and a whole or a constant proportion of the stock produces recruits.

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[1] The biomass ($\boldsymbol{B}(\boldsymbol{F})$) that produces $\boldsymbol{R}(\boldsymbol{F})$ is referred to as $ESB(\boldsymbol{F})$.

Following Francis (1974) and Thompson (1992), the numbers, $N_t(F)$, of individuals in a cohort at age t for a given fishing mortality rate, F, can be written as

$$N_t(F) = R(F)\,e^{-Z(t-t_r)} \tag{A.1}$$

the corresponding cohort biomass, $B_t(F)$, can be written as

$$B_t(F) = w_t R(F)\,e^{-Z(t-t_r)} \tag{A.2}$$

The steady state stock numbers, $N(F)$, during a year when the stock is exploited at F is the sum of average numbers of each age-class (cohort) in the stock exploited at the same fishing mortality rate, F, during that year, which can be written as

$$N(F) = \sum_{a=t_r}^{\lambda} \frac{\int_{t=a}^{a+1} N_t(F)\,dt}{\int_{t=a}^{a+1} dt} = R(F)\int_{t=t_r}^{\lambda} e^{-Z(t-t_r)}\,dt \tag{A.3}$$

The corresponding steady state stock biomass, $B(F)$, is

$$B(F) = \sum_{a=t_r}^{\lambda} \frac{\int_{t=a}^{a+1} B_t(F)\,dt}{\int_{t=a}^{a+1} dt} = R(F)\int_{t=t_r}^{\lambda} w_t e^{-Z(t-t_r)}\,dt \tag{A.4}$$

The mean weight of individuals, $W(F)$, in the steady state stock exploited at F in a given year is

$$\begin{aligned} W(F) &= \frac{B(F)}{N(F)} = \frac{R(F)\int_{t=t_r}^{\lambda} w_t e^{-Z(t-t_r)}\,dt}{R(F)\int_{t=t_r}^{\lambda} e^{-Z(t-t_r)}} \\ &= \frac{Z\int_{t=t_r}^{\lambda} w_t e^{-Z(t-t_r)}\,dt}{1 - e^{-Z(\lambda-t_r)}} \end{aligned} \tag{A.5}$$

Therefore, combining (A.4) and (A.5), the following relationship is obtained:

$$B(F) = \frac{R(F)\,W(F)(1 - e^{-Z(\lambda-t_r)})}{Z} \tag{A.6}$$

The virgin steady state stock biomass, $B(0)$, is then

$$B(0) = \frac{R(0)\,W(0)(1 - e^{-M(\lambda-t_r)})}{M} \tag{A.7}$$

The maximum sustainable yield (MSY) occurs at a fraction, X, of the virgin stock biomass and the MSY-producing equilibrium biomass, $B(F_{MSY})$, can

be expressed as

$$B(F_{MSY}) = XB(0) = X\frac{R(0)\,W(0)(1 - e^{-M(\lambda-t_r)})}{M} \tag{A.8}$$

From Eq. (A.6), it can also be written as

$$B(F_{MSY}) = \frac{R(F_{MSY})\,W(F_{MSY})(1 - e^{-Z_{MSY}(\lambda-t_r)})}{Z_{MSY}} \tag{A.9}$$

The following F_{MSY} to M relationship can be established from Eqs. (A.8) and (A.9):

$$F_{MSY} = \left[\frac{W(F_{MSY})\,R(F_{MSY})(1 - e^{-Z_{MSY}(\lambda-t_r)})}{XW(0)\,R(0)(1 - e^{-M(\lambda-t_r)})} - 1\right] M \tag{A.10}$$

Appendix B. Calculation steps to determine effective spawning biomass-per-recruit $(ESB/R)_F$ for Bristol Bay red king crab

The following assumptions were made to simplify the derivation:

1. Mortality takes place immediately after growth.
2. All female red king crab moult annually, but males moult with a size-dependent moult probability.
3. Instantaneous natural mortality, M, and bycatch mortality, BYM, are constant and independent of size and sex.
4. Instantaneous fishing mortality, F, is constant and independent of size.
5. Instantaneous handling mortality, HM, is constant and independent of size.
6. Recruits deterministically generated from S–R models for per-recruit analysis have 1:1 sex ratio.

Male pre-recruit 1 group consisted of three size-classes ($l = 1$–3). The following models were applied to these size intervals:

• When $l = 1$

$$\begin{aligned} N(0)_{l,t+1} &= N(0)_{l,t}(m_l P_{l,l} + 1 - m_l) \\ &\quad \times e^{-(M + HM\,\delta + BYM)} \end{aligned} \tag{B.1}$$

The above equation is based on a simple cohort decline formula $N(0)_{l,t+1} = N(0)_{l,t}\,e^{-Z}$ with

$N(0)_{l,t}$ adjusted (by the terms inside the brackets immediately after $N(0)_{l,t}$) for proportion of crabs in size-class l remaining in the same size class as a result of moulting (m_l), but with insufficient growth ($P_{l,l}$) to move in to a higher size group, and proportion of nonmoulting ($1 - m_l$) crabs.

• When $l = 2$ and 3

$$N(0)_{l,t+1} = \left[\sum_{l'=1}^{l-1} N(0)_{l',t} m_{l'} P_{l',l} \right.$$
$$\left. + N(0)_{l,t}(m_l P_{l,l} + 1 - m_l) \right]$$
$$\times e^{-(M+HM\delta+BYM)} \tag{B.2}$$

The above equation is based on $N(0)_{l,t+1} = N(0)_{l,t} e^{-Z}$ with $N(0)_{l,t}$ comprised of two components (the terms inside the square brackets): (1) sum of numbers of crabs at lower size-classes (l') that enter the size-class l as a result of moulting ($m_{l'}$) and growing ($P_{l',l}$); and (2) number of crabs remaining in the same size-class l as a result of moulting (m_l), but with insufficient growth ($P_{l,l}$) to move in to a higher size group, and nonmoulting ($1 - m_l$) number of crabs. Eqs. (B.3) and (B.4) can be explained in a similar way.

Male recruit and post-recruit groups comprised of seven length intervals ($l = 4$–10). The following models were applied to these size intervals:

• When $t + 1 = 1$

$$N(0)_{l,t+1} = \sum_{l'=1}^{3} N(0)_{l',t} m_{l'} P_{l',l} e^{-(M+HM\delta+BYM)} \tag{B.3}$$

• When $t + 1 \geq 2$

$$N(F)_{l,t+1} = \sum_{l'=1}^{3} N(0)_{l',t} m_{l'} P_{l',l} e^{-(M+HM\delta+BYM)}$$
$$+ \left[\sum_{l'=4}^{l-1} N(F)_{l',t} m_{l'} P_{l',l} \right.$$
$$\left. + N(F)_{l,t}(m_l P_{l,l} + 1 - m_l) \right]$$
$$\times e^{-(M+F+BYM)} \tag{B.4}$$

Female class 1 and class 2 groups comprised of two and eight size intervals, respectively. The corresponding models for these size intervals are:

• When $t + 1 = 1$

$$N(0)_{l,t+1} = \sum_{l'=1}^{2} N(0)_{l',t} P_{l',l} e^{-(M+HM\delta+BYM)} \tag{B.5}$$

• When $t + 1 \geq 2$

$$N(0)_{l,t+1} = \sum_{l'=1}^{l} N(0)_{l',t} P_{l',l} e^{-(M+HM\delta+BYM)} \tag{B.6}$$

Eqs. (B.5) and (B.6) are also based on $N(0)_{l,t+1} = N(0)_{l,t} e^{-Z}$ with $N(0)_{l,t}$ equals to the sum of numbers of crabs at lower size-classes (l') that enter the size-class l as a result of annual growth ($P_{l',l}$) with a moulting probability of 1.

The HM was defined as a function of F, ignoring M and BYM as follows:

$$1 - e^{-HM\delta} = \tfrac{1}{2} h (1 - e^{-F})$$

Note that the term 1/2 enters the above formula because sublegal males and females catchability was assumed to be 1/2 of that of legal males (see text). Therefore

$$HM = -\frac{1}{\delta} \ln \left(1 - \frac{h}{2}(1 - e^{-F}) \right) \tag{B.7}$$

The $P_{l',l}$ was determined as follows.

Annual growth increment (x) of crab was assumed to have a normal distribution with a mean growth increment $\bar{l}$ and a standard deviation s. Then

$$P_{l',l} = \frac{\int_{l_1-\tau_{l'}}^{l_2-\tau_{l'}} e^{-(x-\bar{l})^2/2s^2} \, dx}{\sum_{l=1}^{n} \int_{l_1-\tau_{l'}}^{l_2-\tau_{l'}} e^{-(x-\bar{l})^2/2s^2} \, dx} \tag{B.8}$$

The male moult probability, m_l, in length-class l was estimated using the logistic function:

$$1 - \frac{1}{1 + g e^{-dCL}} \tag{B.9}$$

The average spawning biomass was calculated in two steps. First, the average mature abundance in numbers for a given male to female mating ratio

was estimated. Second, the effective average stock biomass was calculated in proportion to this abundance. Thus, the average male stock abundance in number (MSSN(F)) for a given F at time $t + 1$ was computed using the following steps:

- When $t + 1 = 1$

$$\bar{N}(0)_{t+1} = \sum_{l'=1}^{3} N(0)_{l',t} \frac{1 - e^{-(M+HM\delta+BYM)}}{M + HM\delta + BYM} \tag{B.10}$$

- When $t + 1 \geq 2$

$$\bar{N}(F)_{t+1} = \sum_{l'=1}^{3} N(0)_{l',t} \frac{1 - e^{-(M+HM\delta+BYM)}}{M + HM\delta + BYM} + \sum_{l'=4}^{10} N(F)_{l',t} \frac{1 - e^{-(M+F+BYM)}}{M + F + BYM} \tag{B.11}$$

and the sum of average mature male abundances in number over the reproductive ages was estimated by

$$\text{MSSN}(F) = \sum_{t=t_r}^{\lambda} \bar{N}(F)_{t+1} \tag{B.12}$$

The average female stock abundance in number (FSSN(0)) for a zero F (since females are not allowed to retain as catch) at time $t + 1$ was computed using the following formulas:

- When $t + 1 = 1$

$$\bar{N}(0)_{t+1} = \sum_{l'=1}^{2} N(0)_{l',t} \frac{1 - e^{-(M+HM\delta+BYM)}}{M + HM\delta + BYM} \tag{B.13}$$

- When $t + 1 \geq 2$

$$\bar{N}(0)_{t+1} = \sum_{l'=3}^{10} N(0)_{l',t} \frac{1 - e^{-(M+HM\delta+BYM)}}{M + HM\delta + BYM} \tag{B.14}$$

and the sum of average mature female abundances in number over the reproductive ages was estimated by

$$\text{FSSN}(0) = \sum_{t=t_r}^{\lambda} \bar{N}(0)_{t+1} \tag{B.15}$$

Note that the male pre-recruit 1 and female class 1 entry age, t_r, was equivalent to the initial maturity age and t_r was arbitrarily set at 0 (see Section 3).

The mating ratio (the number of females that a male can mate during a spawning period) was applied to adjust the average spawning stock abundances to determine effective total spawning stock biomass (ESB(F)) corresponding to a fishing mortality F.

For example, if one male mates with three females during the breeding period, the effective spawning abundance for each sex was estimated as follows:

1. If FSSN(0) $\leq$ MSSN(F), then male effective spawning abundance was set at FSSN(0)/3, and the corresponding female value was set at FSSN(0).
2. If FSSN(0) $>$ MSSN(F), but $(3\,\text{MSSN}(F)) \geq$ FSSN(0), then male effective spawning abundance was set at FSSN(0)/3 and the corresponding female estimate was set at FSSN(0).
3. If FSSN(0) $>$ MSSN(F), but $(3\,\text{MSSN}(F)) <$ FSSN(0), then male effective spawning abundance was set at MSSN(F) and the corresponding female value was set at 3 MSSN(F).

The effective spawning biomass for male (MSSB(F)) was estimated by the following formulas:

- When $t + 1 = 1$

$$\bar{B}(0)_{t+1} = \left[\sum_{l'=1}^{3} N(0)_{l',t} W_{l'} \frac{1 - e^{-(M+HM\delta+BYM)}}{M + HM\delta + BYM} \right] \times \frac{\text{effective MSSN}(F)}{\text{MSSN}(F)} \tag{B.16}$$

- When $t + 1 \geq 2$

$$\bar{B}(F)_{t+1} = \left[\sum_{l'=1}^{3} N(0)_{l',t} W_{l'} \frac{1 - e^{-(M+HM\delta+BYM)}}{M + HM\delta + BYM} \right. \\ \left. + \sum_{l'=4}^{10} N(F)_{l',t} W_{l'} \frac{1 - e^{-(M+F+BYM)}}{M + F + BYM} \right] \\ \times \frac{\text{effective MSSN}(F)}{\text{MSSN}(F)} \tag{B.17}$$

$$\text{MSSB}(F) = \sum_{t=t_r}^{\lambda} \bar{B}(F)_{t+1} \tag{B.18}$$

The corresponding equations for female effective spawning biomass (FSSB(0)) are:

• When $t + 1 = 1$

$$\bar{B}(0)_{t+1} = \left[\sum_{l'=1}^{2} N(0)_{l',t} W_{l'} \frac{1 - e^{-(M+HM\delta+BYM)}}{M + HM\delta + BYM} \right]$$
$$\times \frac{\text{effective FSSN}(0)}{\text{FSSN}(0)} \tag{B.19}$$

• When $t + 1 \geq 2$

$$\bar{B}(0)_{t+1} = \left[\sum_{l'=3}^{10} N(0)_{l',t} W_{l'} \frac{1 - e^{-(M+HM\delta+BYM)}}{M + HM\delta + BYM} \right]$$
$$\times \frac{\text{effective FSSN}(0)}{\text{FSSN}(0)} \tag{B.20}$$

$$\text{FSSB}(0) = \sum_{t=t_r}^{\lambda} \bar{B}(0)_{t+1} \tag{B.21}$$

where, following Beyer (1987):

$$W_l = \left(\frac{1}{\text{CL}_{up} - \text{CL}_{low}} \right) \left(\frac{a}{b+1} \right)$$
$$\times (\text{CL}_{up}^{b+1} - \text{CL}_{low}^{b+1}) \tag{B.22}$$

$$W = a\,\text{CL}^b \tag{B.23}$$

The combined effective total spawning stock biomass-per-recruit $((\text{ESB}/R)_F)$ was determined by

$$\left(\frac{\text{ESB}}{R} \right)_F = \frac{\text{MSSB}(F) + \text{FSSB}(0)}{R} \tag{B.24}$$

where R (number of pre-recruit 1 males plus class 1 females) was fixed at 2000.

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